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BRAINCASTS OF *PHENACODUS, NOTOSTYLOPS,* AND *RHYPHODON*[1]

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The brain is the most important single mammalian organ, and knowledge of any extinct group must be considered very inadequate until it includes some data on the endocranial anatomy. The interest and value of endocranial casts are generally recognized, but their study and description have perforce been rather unsystematic and have not often been correlated with the general course of morphological and phylogenetic investigations. Fossil braincasts are relatively rare and must inevitably be even less common than good skulls and incomparably more rare than good dentitions. The recent comprehensive and invaluable review by Edinger (1929) serves not only as a basis for continuing and systematizing research on braincasts but also as an indication of the more serious gaps in present knowledge.

One of the most important of these gaps concerns the native South American ungulates. In spite of voluminous osteological and dental studies by Ameghino, Scott, Sinclair, and many others, almost nothing has been known of the brain in these groups. Gervais (1872) gave a cursory description and one figure each of the braincasts of two Pleistocene genera, *Typotherium* and *Toxodon,* and I (1932) have briefly discussed very poor natural casts of the Eocene *Notostylops* and *Oldfieldthomasia.* Nothing has been published on braincasts of other groups; in particular, nothing has been known in this respect of any member of the abundant and important Order Litopterna.

It is now possible to describe and illustrate good braincasts of typical members of four major groups of South American ungulates. The Notostylopidae, commonly referred to the Entelonychia but not typical of that suborder, are represented by *Notostylops,* the homalodontotheres, or typical entelonychians, by *Rhyphodon,* the Typotheria by *Hegetotherium* and *Protypotherium,* and the Litopterna by *Proterotherium.* The specimens of the first two genera were collected by the Scarritt Patagonian Expedition. Those of the last three were collected by Barnum Brown in 1899 and were described in the Princeton reports, but brain-

[1]Publications of the Scarritt Patagonian Expedition, No. 15.

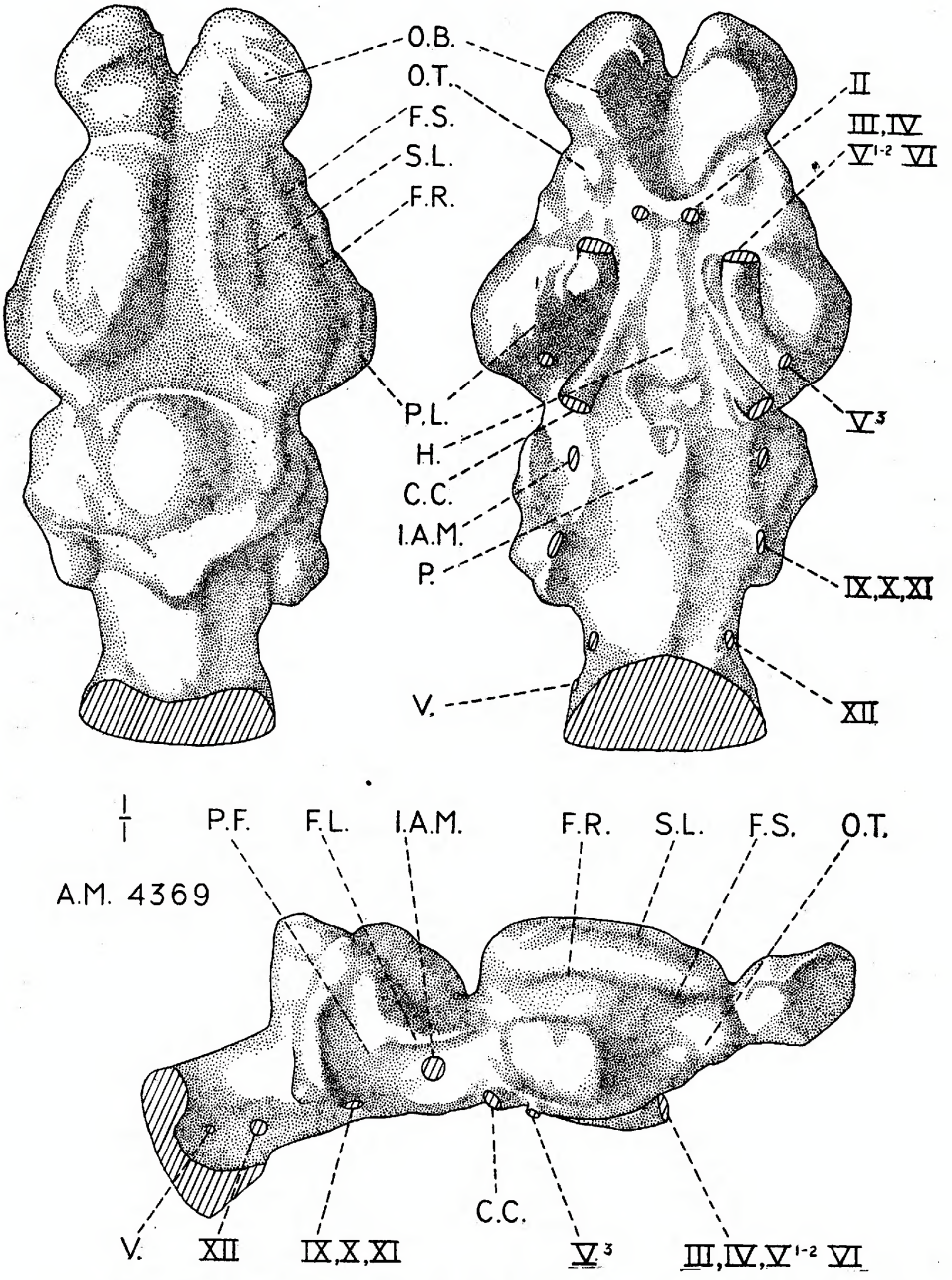

Fig. 1.—*Phenacodus primaevus* Cope. Braincast from Amer. Mus. No. 4369. Dorsal, ventral, and right lateral views. Natural size.

casts were not previously made and are now prepared and studied as part of the research program of the Scarritt Expedition.

In the present paper the braincasts of *Notostylops* and *Rhyphodon* will be described, and as a basis for the study of ungulate braincasts in general, the already fairly well known cast of *Phenacodus* is redescribed and more thoroughly illustrated. In a second paper, to follow immediately, the other South American braincasts are described and the general results given.

It is assumed that the usual conventions of braincast description are accepted. A paleontological braincast, of course, is not a cast of the brain but a mold of the endocranial cavity. In some points it closely approximates the brain but in others may differ widely. The degree and nature of this relationship are generally understood and need not be discussed here. Edinger has admirably summed them up in her comprehensive work.

The casts described in this and the following paper are all artificial, and except for that of *Phenacodus*, made for Cope fifty years ago, were skilfully prepared by Otto Falkenbach. Flexible glue molds were taken from the cleaned cranial cavities, and these were reproduced in plaster for study and preservation. The drawings are by Mildred Clemans. These are diagrammatic to the extent that one side has been used to supplement the other and that artifacts or postmortem injuries are ignored so far as safely possible. Such semidiagrammatic drawings more clearly and accurately represent the original structure than would purely objective reproductions of the casts with all their inevitable accidental imperfections.

Phenacodus

The braincast of *Phenacodus* is of exceptional importance because of its generalized ungulate character. More nearly than any other yet known, it seems to represent the ancestral condition for ungulates in general, as is attested not only by its own structure but also by the broadly proto-ungulate character of the dental and osteological anatomy of this genus. Although in general archetypal, *Phenacodus* is not, of course, really and literally an ancestral ungulate, and the braincast, as well as other features, shows some diagnostic characters of a natural group Condylarthra. These are in part due to the relatively late retention of primitive characters, but in part, and to an extent difficult to define at present, they are more particular and characteristic.

The cast here described is an artificial cast of *Phenacodus primaevus*,

Amer. Mus. No. 4369, and the identical specimen has already been described and figured by Cope (1884), Edinger (1929) and Tilney (1931). In spite of this extensive previous work, the cast is still capable of yielding new facts, especially as full advantage has not previously been taken of the possibility of comparing the cast with the skull from which it came. It may also be useful to gather together all the available data on this crucial form. Cope's description was somewhat cursory and he left many essential features unidentified. Miss Edinger based her work on Cope, nevertheless making some new observations, but falling slightly into error through lack of the original specimen. Tilney was concerned chiefly with the broader features of the cast and did not consider all its details.

Dorsally the cast is very clearly divisible into its three main parts, olfactory bulbs, cerebral hemispheres, and cerebellum, which are arranged serially. The ratio of their lengths is about 2:4:3. The total length (excluding the medulla) is about 70 mm., and the length of the skull was about 237 mm., giving an index[1] of 30. Flexure is very slight: a line continuing the central axis of the medulla oblongata would emerge at the dorsal surface only at the anterior end of the cerebral hemispheres, and one continuing the lower contour of the medulla would emerge at the anterior tips of the olfactory bulbs. Except, probably, for part of the midbrain, none of the dorsal surface has been covered by the expanding neopallium.

The rhinencephalon is very strongly developed, both in bulk and in area constituting well over half of the forebrain. The olfactory bulbs are large and well separated from each other by a median anterior notch. They are divergent, thickened at the anterior end, slightly compressed dorsoventrally, and attached to the cerebrum by short heavy peduncles. As noted by Tilney, obliquely transverse crests on the dorsal surfaces mark the limits of the fibers of the olfactory nerves. Flattened surfaces facing antero-ventro-laterally lay against the cribriform plate. Ventrally a deep triangular fossa, open anteriorly but sharply bounded posteriorly, separates opposite peduncles and the anterior halves of the olfactory tubercles. The latter are distinctly visible as a pair of rather gentle, nearly circular swellings.

The pyriform lobes are even larger than the olfactory bulbs and are visible in dorsal view at the posterolateral parts of the cerebrum, where they form the greatest transverse expansion of the brain.

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[1] $\frac{\text{Brain length} \times 100}{\text{Skull length}}$

Even the neopallium is distinctly narrower anteriorly than posteriorly, but less so than the cerebrum as a whole, due to the strong posterolateral extension of the pyriform lobes. The longitudinal scissure is of remarkable depth and breadth, without distinct signs of the vascular sinus, giving so peculiar an aspect that I suspect it of being in part artificial.[1]

Cope described four convolutions, or gyri, of the cerebrum, stating (1884, p. 441) that "there are three on each side above the sylvian convolution [sulcus?], and a fourth extends from the sylvian upwards and posteriorly below the posterior part of the third or external convolution . . . the internal and external convolutions unite anteriorly, passing round the extremity of the median convolution." Tilney (1931, pp. 455–458) sees doubtful evidence of a single secondary sulcus, the sulcus lateralis, and tentatively considers the hemispheres to have a lateral [or marginal], a supra-sylvian, and an ectosylvian convolution. The interpretation must be in part subjective, for the surface is vaguely irregular without a definite, indubitable pattern. The presence of a sulcus lateralis may be taken as highly probable, and of another sulcus, perhaps a suprasylvian, as possible. The fourth convolution of Cope seems to lie below the rhinal fissure as tentatively recognized by Tilney and by me, and is probably only accidentally (and certainly only very vaguely) separable from the pyriform lobe.

The rhinal fissure seems fairly well defined on the right side, but is very doubtfully recognizable on the left. The fossa sylvii forms a distinct emargination, anterior to the middle of the hemispheres, but is not definitely bounded. It does not appear to be continued into a sulcus.

The fossa hypophyseos was not marked, there being in this region only a broad and gentle convexity. Edinger was misled by the shading of Cope's figure and identified as the hypophysis a light median spot which, in fact, represents not a projection on the cast but a sharp depression posterior to the hypophysis, that is, the depression caused by the posterior clinoid processes.

Cope noted the probability that the corpora quadrigemina were exposed in the prominent space between the cerebrum and cerebellum, but as is almost always true of braincasts, they have left no impression on the bone.

The large cerebellum has well distinguished vermis and hemispheres. The vermis is sharply divided into a large, oval, gently convex

[1]The corresponding bone surface is now visible only obscurely, as it has been so firmly included in the skull reconstruction that the braincase could not again be laid open without serious damage.

anterior lobe and a sharp, conical posterior lobe. On the occipital face is at least one more vague transverse fissure or sulcus. The upper surface of each hemisphere is an irregular plate sloping forward, and ending posteriorly at a fairly sharp angulation between it and the occipital surface. Anterolaterally it is produced into a descending process, elongate anteroposteriorly, lodged in the petrosal, nominally a flocculus.[1] From the posteroexternal angle of the hemisphere another process descends steeply, inclined slightly backward, along the posterior edge of the petrosal fossa, ending at the posterior lacerate foramen.

The pons is indicated by a gentle convexity beneath the anterior part of the cerebellum. The medulla oblongata is nearly smooth and has no surface features of interest.

The nerve exits are all well shown either on the cast or on the original skull. The area of origin of the olfactory fila has already been described. The optic chiasma forms a small swelling on the midline posterior to the olfactory tubercle.

The two optic nerves have distinct but small exits about 4 mm. apart. Along the medial side of the basal aspect of each pyriform lobe, a large ridge, filling of a groove and canal, curves forward and slightly inward, ending in a free projection (filling of a foramen) at the anterior end of the lobe, separated by about 12 mm. from its opposite homologue. These are the courses of III, IV, V_{1-2}, and VI, leading to the anterior lacerate foramen. On the posterior ventral surface of each pyriform lobe, external to the beginning of the large passage just mentioned, is a much smaller, circular, nearly vertical stalk, representing V_3. The internal auditory meatus (VII and VIII) does not show on the cast, but can be recognized in the skull, in the midst of the petrosal (petrosal fossa of the cast) beneath the anterior part of the flocculus. The posterior lacerate foramen (IX, X, XI, and vessels) is large and at the postero-inferior angle of the cerebellum. The condylar foramen (XII), not visible on the cast but clear on the skull, is single and lies at about the middle of the medulla slightly ventral to its most lateral part.

There are only two pairs of impressions definitely and exclusively of vascular origin. On the ventral surface near the junction of fore- and hindbrains, or ventrolaterally between the petrosal fossa and the pyriform lobe, on each side, a large canal begins and curves inward and forward to merge with the convexity of the infundibular region. These

[1]As in most braincasts, the surface detail is insufficiently impressed on the bone for determination of the precise minor structure and convolutions, and hence the exact homologies must remain doubtful. It is necessary to use a somewhat more vague and general nomenclature than that now applied to the details of recent cerebella. This part lodged in the petrosal, for instance, has usually been and may well be called the "flocculus," although it is not strictly or exclusively a true flocculus in every case.

impressions doubtless represent the entocarotids and are large and prominent. Another and much smaller vascular canal is indicated on the medulla, dorso-posterior to the exit of XII[1]. Those of the two sides are not quite symmetrical.

In résumé, the outstanding features of this braincast are:

1. Great length relative to width, the width being contained in the length (exclusive of the medulla) 1.57 times.
2. Full dorsal exposure of olfactory lobes and cerebellum and probable partial exposure of corpora quadrigemina.
3. Large relative size of olfactory bulbs and cerebellum, the dorsal lengths of the bulbs, cerebral hemispheres, and cerebellum being in about the ratio 2:4:3.
4. Nearly serial arrangement of the principal parts.
5. Relatively strong development of the whole rhinencephalon and small neopallium.
6. Slightly gyrencephalic cerebrum.
7. Cerebral hemispheres as a whole strongly pyriform or triangular in outline, with the greatest width posterior.

The principal dimensions are:

Length of skull (slightly restored)	ca. 237 mm.
Total oblique dorsal length of braincast, including medulla oblongata	82.5 mm.
Length between verticals, exclusive of medulla	70 mm.
Length of olfactory bulbs	15 mm.
Width across olfactory bulbs	30 mm.
Length of cerebral hemispheres	30 mm.
Width across cerebral hemispheres (pyriform lobes)	44.5 mm.
Length of cerebellum (vermis)	24 mm.
Width of cerebellum (flocculi)	36.5 mm.
Minimum width of medulla	19 mm.

Notostylops

I have elsewhere (Simpson 1932) described a partial natural braincast of *Notostylops*. The natural cast (Museo Nacional, Buenos Aires, No. 10506) had the cerebellum very poorly preserved and did not reveal the ventral surface or any nerve exits, and the present specimen is therefore much more satisfactory, although also imperfect in some details. The two specimens differ somewhat, most obviously in the greater post-cerebral length of the present cast. In this respect I believe it to

[1]Cope (1884, p. 437) was doubtless referring to this when he said, "the *F. condyloideum* enters the foramen magnum at the middle of its side, and is small. . . . " This is not the anterior condylar-foramen, or hypoglossal canal, which does not show on the cast (although well preserved on the skull) and has not previously been identified.

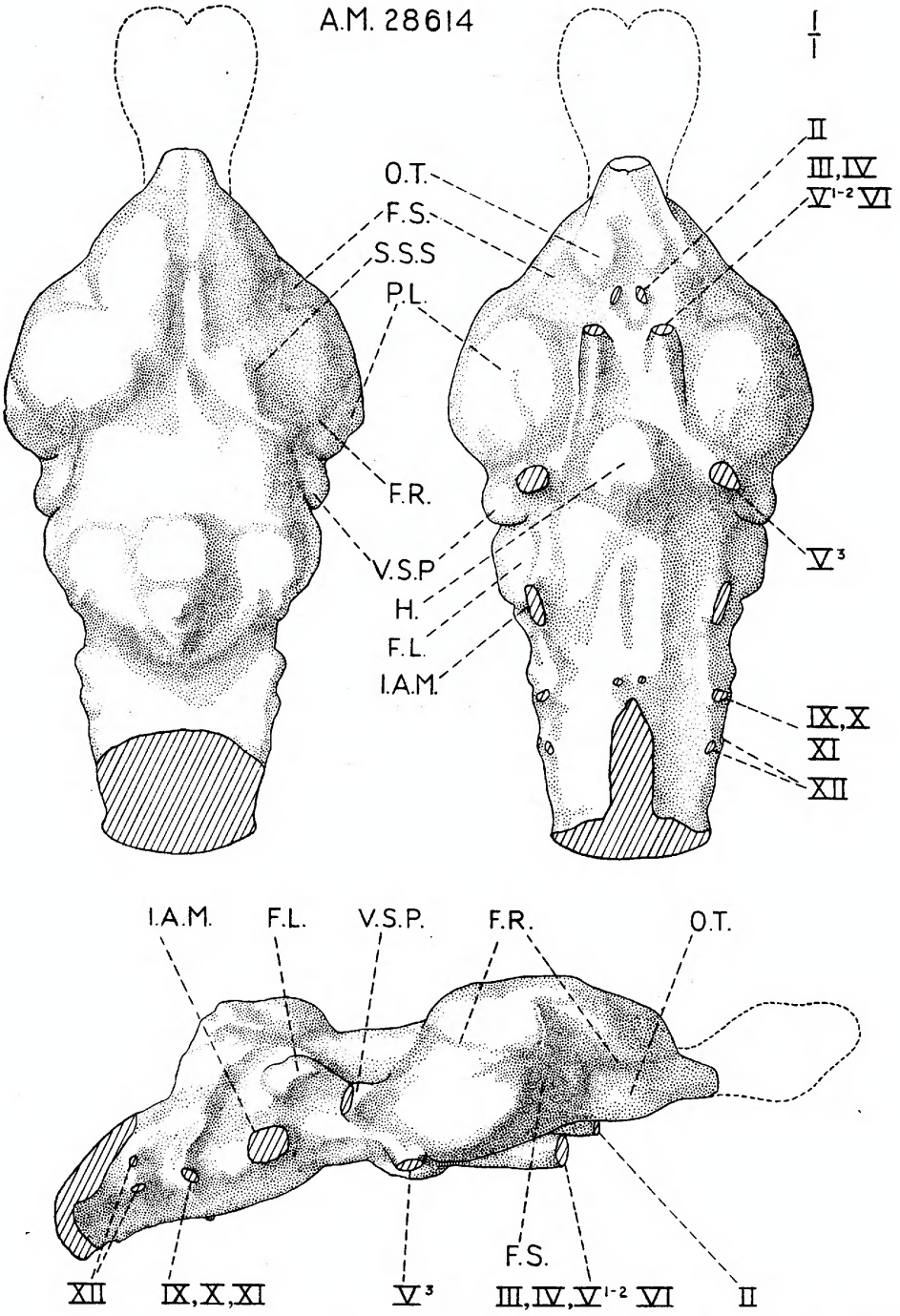

Fig. 2.—*Notostylops* sp. Braincast from Amer. Mus. No. 28614. Dorsal, ventral, and right lateral views. One and one-half times natural size.

be more primitive and perhaps more typical of the whole genus, although perhaps a little exaggerated. The causes of this disagreement are probably four-fold: (1) the species are different, the present cast being from a species evidently more primitive in characters other than the braincast, (2) the individuals are of different ages, the Buenos Aires specimen older at time of death, (3) the preservation and mode of preparation is different and both are somewhat crushed, in different ways, and (4) in details such as size and clarity of vascular impressions, etc., there was doubtless large individual variation.

This specimen is an artificial endocranial cast of a skull of *Notostylops*, Amer. Mus. No. 28614, found by me in Cañadón Vaca, Chubut, Argentina. It is somewhat crushed dorso-ventrally, most of the left side is lacking, and it was not possible to free the olfactory bulbs, which were very difficult to reach with tools and were filled with barite crystals. Yet all the essential characters posterior to the olfactory bulbs are well shown.

The estimated total length of the skull is 115 mm., and of the brain, exclusive of medulla, 55 mm., giving an index of 48. Even apart from the influence of brain structure, this larger index does not necessarily indicate a larger effective brain capacity than in *Phenacodus*. *Phenacodus primaevus* is twice as large in linear dimensions, and larger animals have relatively smaller brains, other things being equal, and it also has an elongate snout, tending to give low index, while that of *Notostylops* is abbreviated, tending to give a high index. The effective brain size, if a name may be applied to a factor so elusive and so impossible to separate from other and even more important factors of brain development, was probably about the same in the two animals.

The serial arrangement is about as in *Phenacodus* and the flexure is, if anything, slightly less. Olfactory bulbs and cerebellum are as fully exposed, and the midbrain apparently even more so. The ratio of olfactory bulbs, cerebrum, and cerebellum was about 2:4:2, the difference from the 2:4:3 of *Phenacodus* being due to the large dorsal gap between cerebrum and cerebellum, part of which doubtless belongs to the cerebellum although not included in its measurement.

The rhinencephalon is very strongly developed, as in *Phenacodus*. In the Buenos Aires specimen, and also in this as far as can be judged from the skull, the olfactory bulbs are comparable to *Phenacodus* in bulk, but longer, narrower, less divergent, and with more slender peduncles. The olfactory tubercles are relatively even larger and more definite than in *Phenacodus*. The pyriform lobes are equally large and

prominent, but this is due rather to their expansion vertically and posteriorly than to their dorsal exposure, or lateral expansion, for in dorsal view they are more limited than in *Phenacodus*, and chiefly posterolateral and posterior rather than definitely lateral to the neopallium.

The neopallium is even more distinctly triangular than in *Phenacodus*, with the anterior end much narrower than the posterior. The longitudinal scissure is well defined, but not so abnormally developed as in *Phenacodus*, and a vague trace of the venous sinus, at its posterior division point, is visible. The nearly straight and horizontal rhinal fissure is distinctly recognizable. The region of the fossa sylvii is a large ventrolateral depression, and from it a broad, short fissure extends upward and backward. Still more posteriorly, on the posterior part of the neopallium, is a broad and vague depression or sulcus apparently running forward and inward to or toward the upper end of the fissura sylvii, but the details are not impressed on the bone with sufficient definition to determine their exact relationships. On the present specimen there is very vaguely visible but on the Buenos Aires specimen quite distinctly developed, a simple, sagittal sulcus lateralis. The neopallium thus has two longitudinal dorsal gyri, marginal and suprasylvian, and distinct frontal and temporal lobes, the latter larger.

In the Buenos Aires specimen a large blood-vessel follows approximately the course of the rhinal fissure. What may be the homologous vessel in this specimen seems to be faintly indicated at the posterolateral corner of the cerebrum, immediately below the rhinal fissure. A small vessel ascends the anterior surface of the temporal lobe, just behind the fissura sylvii.

A round median swelling on the ventral surface, between and slightly posterior to the pyriform lobes, indicates the fossa hypophyseos, which is considerably more definite than in *Phenacodus*.

Laterally the flocculi and pyriform lobes are only about 2 mm. apart, but dorsally, between the anterior end of the vermis and a line tangent to the posterior ends of the temporal lobes, about 6.5 mm. intervenes between cerebrum and cerebellum. In this space is a broad, roughly rectangular, almost flat, depressed area. Here the midbrain must have been exposed, and the corpora quadrigemina were probably clearly visible in the dorsal view of the original brain, but they have left no impression on the bones. Probably part of the cerebellum underlay this area also, but in this specimen, not yet fully adult, it had not yet modeled the overlying bone.

The cerebellum is clearly divided into a large vermis and relatively

very small hemispheres. The vermis is divided by two real but indefinite transverse sulci into three lobes. These are probably the true anterior, median (simplex), and posterior (posteromedian) lobes and their divisions the fissura prima and fissura secunda, but this is not absolutely certain, as these primary cerebellar fissures are not invariably more prominent than secondary sulci. The anterior lobe is evenly convex and nearly circular in section. The median lobe is also featureless (in the cast), confined to the dorsal surface, and is transverse, about half as long as the anterior lobe. The posterior lobe has about the same length as the anterior, but is less even, with vague traces of transverse sulci, and lies almost entirely on the more vertical occipital exposure of the cerebellum.

The cerebellar hemispheres are very vaguely divided into anterior and posterior moieties on the dorsal and occipital surfaces. Below the anterior part and extending still farther forward is the strongly developed "flocculus," elongated anteroposteriorly. From the posterior lobe of the cerebellar hemisphere, a sharp crest runs downward and backward, bounding the posterior end of the petrosal fossa.

The region of the pons is peculiarly marked by two well defined longitudinal ridges.

The nerve exits are all well shown. The optic chiasma and optic canals occupy the same positions as in *Phenacodus* and the strong canal for III, IV, V_{1-2}, and VI, leading to the anterior lacerate foramen, is also very similar although relatively slightly closer to the midline. V_3 also has the same position and relationships as in *Phenacodus*. The large internal auditory meatus (VII, VIII) is ventral to and in part slightly posterior to the flocculus, near the center of the well defined periotic fossa. Posterior and slightly ventral to it, at the lower end of the post-periotic crest from the cerebellar hemisphere, is the relatively small posterior lacerate foramen (IX, X, XI), quite as in *Phenacodus;* XII also is as in *Phenacodus*, except that it has a second smaller and more dorsal root.

In or near the fossa sylvii there appears to be a small vascular foramen, not very clearly or certainly shown because of slight breakage in this region. The strong entocarotid vessels seen in *Phenacodus* are here absent, doubtless displaced by the development of the bullae. There is a pair of small vascular foramina in the basioccipital near the midline, slightly anterior to the level of the posterior lacerate foramen.

The most prominent vascular opening is directed backward from the posteroexternal angle of the cerebrum, just below the rhinal fissure.

I was at first inclined to consider this an artifact, but its presence and clearly natural character in the Santa Cruz typotheres (see below) confirms its reality as an original endocranial feature. From it comes the great blood sinus so prominent near or on the rhinal fissure in the Buenos Aires specimen and also present, but less obvious, on the present cast. This prominent venous foramen apparently communicates with the epitympanic sinus, the postglenoid foramen, or both. Its relationships may be cleared up more fully by a detailed study of early notoungulate skull structure now in progress. It seems to be an important and unusual character.

Despite the inevitable differences of preservation, the brains of *Phenacodus* and of *Notostylops* are seen to be remarkably similar. The general proportions, degree of development, and many details are closely comparable and the differences are mostly minor and not greater than may commonly be seen between the braincasts of members of a single family. While the skull of *Notostylops*, and its teeth, have been rather strongly modified, the brain is conservative and clearly has progressed hardly at all beyond the primitive ungulate type, apparently also retaining evidence of some special affinity with *Phenacodus*, or with the Condylarthra in general.

Among the numerous details in which *Notostylops* differs from *Phenacodus*, the following seem to be the most definite and important:

1. Braincast slightly longer in proportion to its width.
2. Olfactory bulbs of different shape (see above).
3. Pyriform lobes extending somewhat more posteriorly and less laterally.
4. Neopallium more triangular in outline.
5. Gyri probably developed in much the same pattern and to about the same degree, but some difference in detail not excluded by the known material.
6. Fossa hypophyseos relatively deeper and more distinct.
7. Cerebellum shorter relative to cerebrum.
8. Pons underlain by two longitudinal ridges (vessels?).
9. Hypoglossal canal double (at internal end).
10. Course of entocarotid different.
11. Large vascular opening at posterolateral angle of cerebrum.

Several of these characters, perhaps most of them, are due to or related to relatively superficial habitus changes, shape of skull, development of bullae, etc., rather than to any more deep-seated or phyletic distinction.

The principal dimensions are:

Length of skull (estimated, rostrum imperfect)	ca. 115 mm.
Length of braincast exclusive of medulla (estimated, olfactory bulbs absent)	ca. 55 mm.
Length of olfactory bulbs (estimated[1])	ca. 12 mm.
Length of cerebral hemispheres	23 mm.
Width across cerebral hemispheres (pyriform lobes)	30 mm.
Length of cerebellum (vermis)	13 mm.
Width of cerebellum (flocculi)	23 mm.

Rhyphodon

The little-known genus *Rhyphodon* Roth (with its equally neglected synonyms *Pehuenia* and *Setebos*) is represented by fairly good skulls and dentitions in the La Plata collection, but has been described only in the briefest fashion, and only the upper dentition (*"Pehuenia wehrlii"*) has been figured. It is a homalodontothere, probably not directly ancestral to *Homalodontotherium* but a member of the same family. Its brain may be considered representative of the early true entelonychians (in the most limited sense).

The present braincast is from a partial skull, Amer. Mus. No. 29414, found by C. S. Williams in the *Astraponotus* Beds near the Cerro del Humo, north of the Cuenca de Sarmiento, Chubut, Argentina. I believe this to be the type locality of *Rhyphodon lankesteri* and its synonyms. Roth labeled them as from the Cretaceous of Lago Musters, but for reasons too lengthy to detail here, it seems almost certain that they are really from the *Astraponotus* Beds (Eocene or possibly early Oligocene) of the Cerro del Humo. This skull has the complete cranium, also much of the right frontal, nasal, and premaxilla, and a fragment of the maxilla, without any teeth. Identification is not certain, but it is surely a very close relative of *Rhyphodon* and probaby belongs to that genus, perhaps to its type species, *R. lankesteri*. The bone is very brittle and chalky and the cranium somewhat broken and eroded, but most of the essential characters of the braincast are determinable by comparing the two sides and the skull. The cast is artificial, taken by sawing the cranium on the midline in a vertical sagittal plane.

The total length of the skull (slightly crushed and tip of premaxilla missing) was about 230 mm., and of the brain, exclusive of the medulla, about 85. The index is thus 37. Allowing for the large size (tending to give a small index) and the short rostrum (tending to give a large index),

[1]This cannot be far from the correct measure, as both anterior and posterior boundaries are visible in the skull, although the distance between them cannot be measured directly or exactly, and the ratio is about as in the Buenos Aires specimen.

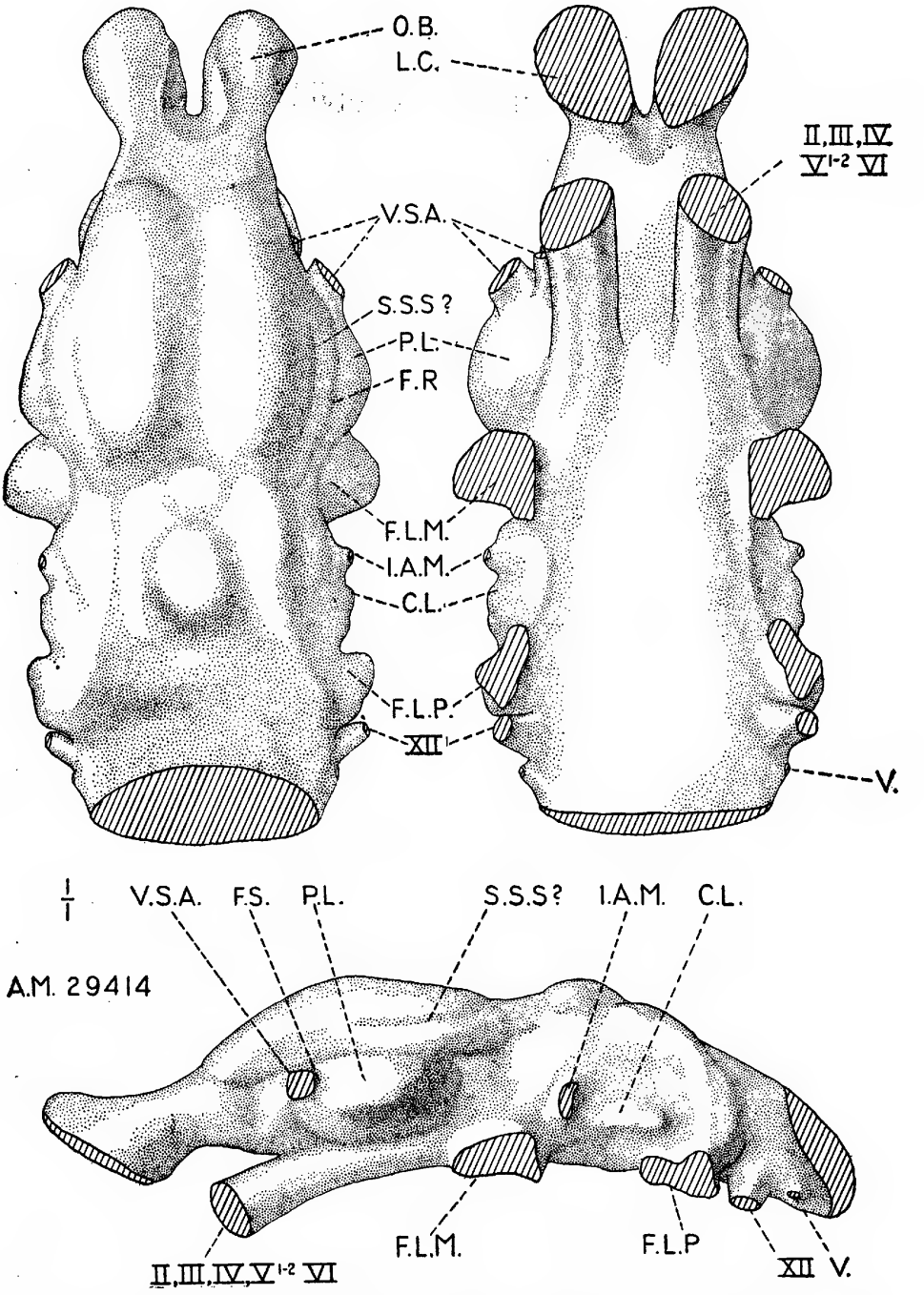

Fig. 3.—*Rhyphodon* sp. Braincast from Amer. Mus. No. 29414. Dorsal, ventral, and left lateral views. Natural size.

and for the general proportions of the brain itself, this probably indicates an effective brain size not significantly different from *Notostylops* (48, made large by small size and short rostrum) or *Phenacodus* (30, made small by large size and long rostrum), so far as such a necessarily very rough estimate can be made.

The arrangement seems to be about as serial as in *Phenacodus* or *Notostylops*, and the flexure about as in the latter, except that the olfactory bulbs are bent downward (they are overlain by large frontal sinuses absent in the other genera here described). The ratio olfactory bulbs: cerebrum: cerebellum is roughly 3:8:6, rather closely paralleling *Phenacodus* or *Notostylops*, but with relatively somewhat smaller olfactory bulbs. The maximum cortical width is contained almost exactly twice in the length, making the brain as a whole relatively more elongate than in *Phenacodus* and less than in *Notostylops*. The most unusual feature of the general proportions is that the cerebellum is almost as wide as the cerebrum.

The olfactory bulbs, fully exposed and large although relatively smaller than in *Notostylops*, are of almost equal width, length, and depth. They are completely separated by a deep narrow fissure, which does not, however, split the strong peduncles. The olfactory tubercles, while visible, are not prominent and are more poorly defined than in *Notostylops*. The pyriform lobes are about as prominent as in *Phenacodus* or *Notostylops*, or possibly slightly weaker relatively, and are visible in dorsal view, extending laterally to the neopallium as in *Phenacodus* rather than posteriorly as in *Notostylops*.

The neopallium, while longer and narrower than in *Phenacodus*, has the less strongly triangular outline of that genus, the anterior and posterior widths being less disparate than in *Notostylops*. The rhinal fissure is nearly straight, continuous, and horizontal. The fossa sylvii is placed as in *Notostylops*. Imperfections of the bones make it impossible to say whether it is produced into a fissure, but if present this must have been shallow and short. The neopallium is almost perfectly smooth, the only evidence of a sulcus being a short, straight, very shallow and vague longitudinal depression 6 mm. above the rhinal fissure and about 15 mm. from the midline. If this is a sulcus, it seems to correspond more nearly with the (nominally) suprasylvian sulcus of *Notostylops*. If this is true, its development without a sulcus lateralis is unusual, and if it is the sulcus lateralis, its very lateral position is even more extraordinary. The region of the hypophysis is imperfect, but it is evident that the fossa hypophyseos was even smaller and shallower than in *Phenacodus*.

There is a depressed dorsal area between cerebrum and cerebellum, and the midbrain may have been exposed, but if so, the exposure was small.

The whole cerebellar region is very vague and lacks definite character; this is in part due to the imperfection of the bone surface, but even where this is completely preserved the sculpture is slight and indefinite. The occipital exposure is strongly inclined forward and not distinctly differentiated from the dorsal exposure, as it is in *Phenacodus*, *Notostylops*, or indeed most other mammals. Near the junction of these two planes, a division into a large vermis and smaller hemispheres is vaguely seen, but otherwise these surfaces lack definite characters. In lateral view there is a very marked difference from *Phenacodus*, *Notostylops*, and most other primitive ungulates in that there is a lobe of the cerebellum lodged in a fossa of the petrosal posterior and slightly ventral to the internal auditory meatus but very little or probably none dorsal or dorsoanterior to the meatus in the region of the flocculus. I am unable to homologize or interpret this condition, but it seems to be indicated by unbroken bone surface in the skull. As in *Phenacodus* and, less markedly, *Notostylops*, another descending lobe or fissure filling curves to the foramen lacerum posterius around the posterior margin of the petrosal fossa.

The cranial exits are remarkable. There is no definite indication of the optic chiasma, and no trace of an optic canal or foramen can be seen. The optic nerves must have left the brain in a common tunnel with the other nerves destined for the orbit, III, IV, V_1, and VI. But in *Pleurostylodon*, a more primitive relative of *Rhyphodon* from the *Notostylops* Beds, there is a separate optic foramen. The condition in *Homalodontotherium* and other later entelonychians is unknown to me.

The paired projections leading to the anterior lacerate foramina are of enormous size. They carried a complex of nerves, certainly III, IV, V_1. and VI and almost surely also II and V_2. Their compound nature is indicated by a longitudinal groove on the ventral face of each. The stalks representing the median and posterior lacerate foramina are larger on the cast than they would be had not the tympanic bulla been destroyed and a large postmortem gap created between the periotic and the basioccipital-basisphenoid. V_3 clearly passed out through the gap now confluent with the median lacerate foramen, but doubtless had a more exclusive exit when the bone was complete. As usual, IX, X, and XI undoubtedly left through the posterior lacerate foramen. The internal auditory meatus, VII and VIII, is at a relatively high position,

more on the lateral than on the ventral surface of the cast; XII is large and is immediately posterior to the posterior lacerate foramen.

In the region of the fossa sylvii on the left side is a heavy stalk, representing a skull canal which branches in the bone and appears externally as two foramina, a smaller one immediately above the anterior lacerate foramen and a larger dorso-postero-external to this. On the right side there are similar foramina on the external surface of the skull, but the canal fillings have separate origins on the cast. This asymmetry may be, but does not seem to be, due to breaking away of the common part of the canal on the right side. Attempts were made to homologize these with nerve exits, and particularly to homologize the smaller foramen with the optic foramen, but the point of origin on the cast, the course and branching of the canal, and the position of the external foramina would all be so anomalous for cranial nerves that this hypothesis is hardly tenable. These unexpected and prominent canals are more probably of vascular origin. This is also supported by the presence of similar but variable openings in this region in *Pleurostylodon* and some other early entelonychians, even more difficult to interpret as anything but vascular. The possible (but uncertain) occurrence of a very much smaller single opening in the same region in *Notostylops* suggests correlation with this condition, but on such poor data as to be only a suggestion. In any case the difference between the two is very marked. The prominent posterolateral vascular passage from the cerebral chamber in *Notostylops* (and some typotheres) is absent in *Rhyphodon.*

By classifications currently accepted, *Notostylops* and *Rhyphodon* belong to the same suborder, Entelonychia, while *Hegetotherium* and *Protypotherium* belong to a different suborder, Typotheria. The braincasts do not support this arrangement. Whether other and possibly more important characters do make this classification acceptable may be discussed elsewhere, and it suffices here to record that the typothere braincasts examined are more specialized (as they are younger) but seem to agree basically with *Notostylops*, while the braincast of *Rhyphodon* is equally unspecialized but seems to differ significantly from that of *Notostylops.*

Among the differences from *Notostylops* are:

1. Olfactory bulbs relatively smaller.
2. Olfactory bulbs bent downward.
3. Cerebellum relatively larger and width nearly equal to length.
4. Olfactory tubercles less distinct.
5. Pyriform lobes expanded laterally, not posteriorly.

6. Less disparity between anterior and posterior widths of neopallium.
7. Cerebral hemispheres possibly less and differently convoluted.
8. Flocculus not lodged in petrosal, but a petrosal lobe present posterior to the internal auditory meatus.
9. No separate optic canal, and common canal for III, IV, etc., of enormous size.
10. Large double or branching canal to the outside of the skull in the region of the fossa sylvii.
11. No posterolateral cerebral venous canal.

This markedly different character, without departure from about the same primitive developmental level, was altogether unexpected. It will be important to have it confirmed or modified by other entelonychian casts (not at present available to me), but that a decided difference does exist seems to be established.

Some of the dimensions follow:

Width of skull (partly estimated)	ca. 230 mm.
Length of braincast (excluding medulla)	85 mm.
Length of olfactory bulb	14 mm.
Width across olfactory bulbs	28 mm.
Length of cerebral hemispheres	41 mm.
Width across pyriform lobes	43 mm.
Length of cerebellum	30 mm.
Width of cerebellum (exclusive of expansion at posterior lacerate foramen)	39 mm.

Due to crushing and some vagueness of boundaries, none of these figures is exact.

Abbreviations on Text Figures

II—Optic nerves (filling of optic canal).

[II], III, IV, V_{1-2}, VI—The common canal of these cranial nerves, and filling of the anterior lacerate foramen.

V_3—Mandibular nerve (filling of foramen ovale).

IX, X, XI—Point of exit of these nerves (filling of foramen lacerum posterius).

XII—Point of exit of this nerve (filling of hypoglossal canal or condylar foramen).

C.C.—Carotid canal.

C.L.—Cerebellar lobule lodged in petrosal posterior to internal auditory meatus.

F.L.—"Flocculus," or cerebellar lobule in petrosal anterior to internal auditory meatus.

F.L.M.—Foramen lacerum medium.

F.L.P.—Foramen lacerum posterius.
F.R.—Rhinal fissure.
F.S.—Fossa sylvii.
H.—Filling of fossa hypophyseos.
I.A.M.—Internal auditory meatus (nerves VII and VIII).
L.C.—Surface applied to lamina cribrosa.
O.B.—Olfactory bulb.
O.T.—Olfactory tubercle.
P.F.—Petrosal fossa (of cast, not a fossa in the petrosal).
P.L.—Pyriform lobe.
S.L.—Lateral sulcus.
S.S.S.—Suprasylvian sulcus.
V.—Minor vascular foramina.
V.S.A.—Anterior foramina, probably vascular.
V.S.P.—Posterior venous passage from cerebral fossa.

REFERENCES

COPE, E. D. 1884. 'The Vertebrata of the Tertiary Formations of the West.' Rept. U. S. Geol. Surv. Terr. (Hayden), III.

EDINGER, T. 1929. 'Die fossilen Gehirne.' Zeits. gesamte Anat., III Abt., Ergeb. Anat. Entwick., XXVIII, pp. 1–249.

GERVAIS, P. 1872. 'Mémoire sur les formes cérébrales propres à différents groupes de mammifères.' Journ. de Zool., I, pp. 425–469.

SIMPSON, G. G. 1932. 'Skulls and Brains of Some Mammals from the *Notostylops* Beds of Patagonia.' Amer. Mus. Novitates, No. 578.

TILNEY, F. 1931. 'Fossil Brains of Some Early Tertiary Mammals of North America.' Bull. Neurol. Inst. New York, I, pp. 430–505.